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THE LITOPTERNA.

BY E. D. COPE.

THERE has been known for many years a mammal of the Pampean formation of Buenos Ayres called by Professor Owen Macrauchenia.[1] It is distinguished by many peculiarities, but at the time of its first description its characters were chiefly known from the skull and cervical vertebræ. The former resembles very much that of a horse, but has the strange peculiarity of having the external nostrils posterior to their usual position in land mammals,—that is, between the eyes, where it is placed in the sea-cows or manatees. The teeth were generally found much worn, but their general appearance was like those of primitive three-toed horses ; but the canines were small and like the premolars. The cervical vertebræ, on the other hand, displayed characters like those found in the camels, especially in the absence of an especial canal for the vertebral artery, which presumably ran in the canal of the spinal cord. The position of this animal was absolutely uncertain, on account of the absence of specimens of the feet; but Professor Owen was inclined to place it in the Perissodactyla, and other authorities have followed him (Plate XVII.).

Professor Burmeister, of Buenos Ayres, later obtained still better specimens, which included parts of the hind feet. He found that it had three toes on both feet, and he published a restoration of it. He represented it as a long-legged and long-necked mammal, furnished with the short proboscis of a tapir.[2] Within a few years good specimens of the fore feet were received in Paris, and Messrs. Scott and Osborn have given us a figure of that member, which, with what was known before of the hind foot, enables us to place the genus finally in the system. The carpus and tarsus are both taxeopodous, or with the bones of the two rows in continuous lines and not alternating.[3] So this genus is a taxeopod, and cannot enter the Perissodactyla, which is diplarthrous.

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[1] Zool. of the Voyage of the " Beagle," Fossil Mammalia, p. 35, Pl. v. and xv., 1389.

The lamented French paleontologist, Bravard, who perished in the earthquake at Mendoza, thought he had discovered in Argentina species of the European genera Palæotherium and Anoplotherium, which were found by Cuvier in the Eocene deposits near the city of Paris. The discovery of these genera in this region was unlooked for, and its announcement excited much curiosity, if not credence.

In 1873 Prof. W. H. Flower described and figured in the Philosophical Transactions of London (p. 173) the dentition of a new mammal, under the name of *Homalodontotherium cunninghamii.* He regarded it as allied to Rhinoceros on the one hand and Macrauchenia on the other (Fig. 4).

Some years after this Burmeister announced the finding by Moreno of the skull of a large mammal in the Eocene beds of Patagonia, of remarkable character. It was represented as having large and formidable canine teeth and a very short series of molars, but of its affinities no definite idea was expressed. It was named *Astrapotherium patagonicum.*

In the great work on the "Extinct Mammalia of Argentina," recently issued by Ameghino, which is reviewed in the present number of the NATURALIST, the characters of these forms are much more completely described than previously, and the relations of several of them have been clearly pointed out. Information is furnished which enables us to estimate the position of them with certainty. In the year in which this volume was issued the present writer published in the NATURALIST a "Synopsis of the Families of the Vertebrata" (1889). Here the results of my study of the preliminary papers of Ameghino and Burmeister were embodied in the following systematic form. The Macraucheniidæ were placed in the suborder Toxodontia (p. 28). Ameghino having shown that the supposed Palæotherium and Anoplotherium of Bravard were allied to this family, and should be referred to the genera Proterotherium and Oxyodontotherium, a family, Proterotheriidæ, was proposed for the former, and it was also placed in the Toxodontia. The Toxodontia were placed in the Taxeopoda. Ameghino's researches having shown that the fore-foot structure of the Toxodontidæ and Mesotheriidæ is that of the Amblypoda, while the posterior foot only has the taxeopod structure, it became evident that the Toxodontia must be regarded as a distinct order between the Taxeopoda and the Amblypoda. The Proterotheriidæ and Macraucheniidæ having the taxeopod structure of both extremities, must remain where I placed them. M. Ameghino, disregarding the question of taxeopody and diplarthry, places these families under the Perissodactyla, and proposes to regard them as a suborder, with the name of the Litopterna. This name will be retained, and will apply in my system to a suborder of the Taxeopoda.

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[2] Annal. del Mus. Pub. de Buenos Ayres, T. I., p. 32, Pl. I.-IV.; p. 252, Pl. XIII.

[3] Transactions of the Amer. Philos. Soc., 1889, Vol. XVI., p. 540.

The structure of the feet of the Astrapotheriidæ remains unknown. Their location will depend entirely on the solution of this question. M. Ameghino places them in the Amblypoda. This position is rendered extremely improbable by the structure of the true molar teeth. Those of Astrapotherium resemble those of the Toxodontia, but still more those of Macrauchenia. Homalodontotherium resembles Rhinoceros. Until the question is positively settled by the discovery of the feet, I place them in the Litopterna as their most probable position, following Ameghino, so far as regards Homalodontotherium, which he places here.

The suborder Litopterna is nearly related to the Condylarthra, and it is probable that future discovery will obliterate the differences which we find to characterize the known types. The prime characters in which the Litopterna differ from the Condylarthra are the absence of epitrochlear foramen of the humerus, and the ginglymoid articulation of the astragalus with the navicular in one, the anteroposterior, plane. In the Condylarthra this articulation is ball and socket, or nearly universal, as in the Unguiculates generally. The articulation in the Litopterna is of ungulate character, and has the same functional value in the fully developed forms, such as Epitherium, as in the Artiodactyla. In the known forms the fibula articulates with the calcaneum, another point in which they differ from the Condylarthra. A peculiar character, said by Ameghino to characterize this suborder, is the presence of four roots of some of the inferior premolars and molars. This authority also states that they do not possess a clavicle.

The three families differ as follows.

Superior molars essentially tritubercular, the two external cusps modified into Vs; inferior molars with Vs;	*Proterotheriidæ.*
Superior molars with straight external wall and cross-crests, no Vs;	*Astrapotheriidæ.*
Superior molars with subequal external Vs and cross-crests; inferior molars with Vs;	*Macraucheniidæ.*

The dentition of the Proterotheriidæ could be easily derived from that of the Periptychidæ of the Condylarthra by the modes of complication usual in other Ungulata. On the other hand that of the Macraucheniidæ could have been derived from that of the Meniscotheriidæ. The dental type of the Astrapotheriidæ could have been derived from that of Protogonia by a process similar to that by which the Rhinocerotine line arose from a primitive quadritubercular diplarthrous form. The parallel presented by the succession of the Litopterna in time as compared with that of Diplarthra is most remarkable. The resemblances in the dentition are such that the early students of the paleontology of Argentina referred members of the Proterotheriidæ and Macraucheniidæ to the Perissodactyla and Artiodactyla, and later authors have referred one of the Astrapotheriidæ to the Rhinocerotidæ. In the last case the resemblance may be traced in all parts of the molar teeth, even including the plication of the anterior part of the external wall of the crown. The entire suborder is a remarkable illustration of the identity of results produced by identical mechanical causes. The parallel is further increased by the diminution in the number of the digits, in the cases when the structure is known, in the course of geologic time.

The families range from the Lower Eocene to Plistocene time. They have not been found hitherto outside of South America. They thus continued much longer than the Condylarthra, and must be regarded as a derivative of that suborder, which found in South America conditions favorable for continuance which were wanting in North America.

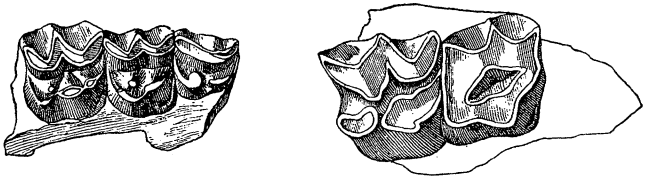


FIG. 1.—*Proterotherium ? cavum* Amegh.; last three premolars, grinding face; natural size. FIG. 2.—*Epitherium laternarium* Amegh.; true molars, from below; natural size. Both from Ameghino.

I now consider their characters in greater detail.

In the PROTEROTHERIIDÆ we have a type more closely connected with the Periptychidæ of the Condylarthra than any later form. The superior molars are tritubercular, the protocone with well-developed accessory tubercles anteriorly and posteriorly, as in Periptychus. The external cusps of these teeth are modified into Vs, however, as in Meniscotherium. The three internal cusps become confluent on wear (Figs. 1, 2).

The genera distinguishable in the material furnished by M. Ameghino are as follows:

Digits? Symphysis not coössified; no intermediate tubercles of the superior molars;	*Proterotherium* Amegh.
Like the last, but intermediate tubercles present;	*Anisolophus* Burm.
Symphysis mandibuli coössified;	*Thoätherium* Amegh.
No intermediate tubercles; ? symphysis; three digits, the lateral rudimental;	*Epitherium* Amegh.

It is not yet possible to determine the number of digits present in the greater number of the genera of this family. It is, however, extremely probable that we have four or five in the Eocene genera Anisolophus and Thoatherium. If so, we have a successional reduction in later periods, similar to that which has been shown to have occurred in the horse line. In Epitherium Amegh. we reach a stage corresponding to that of Hippotherium, the lateral digits being reduced to the condition of dew-claws, according to Ameghino (Fig. 3). Proterotherium and Anisolophus are the only genera in which the dentition is well known, and our knowledge is confined to the molars. The premolars nearly resemble the true molars in both jaws.

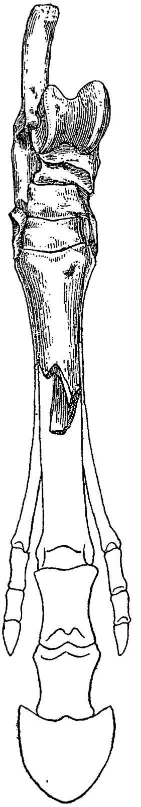


Fig. 3.—*Epitherium laternarium* Amegh.; right posterior foot; two-fifths natural size. From Ameghino.

Two species certainly belong to Proterotherium, and they are from the "inferior Oligocene" of Patagonia. Three other species from the Oligocene and Eocene of the same region, described under distinct generic names by Ameghino, have not been yet clearly distinguished from Proterotherium. Two species are referred to Anisolophus, which with the single one of Thoatherium are from the Eocene. But one species of Epitherium (*E. laternarium* Amegh.) is yet known. This is a most interesting animal, and took the place in the Miocene fauna of Argentina (according to Ameghino) of the three-toed horses in the corresponding age in the Northern Hemisphere. It was about the size of a small guanaco, and was digitigrade, like the higher Diplarthra.

In the MACRAUCHENIIDÆ we have a line of modification different from that of either of the other two families, resembling in some respects both of them. Thus the superior molars are constructed on the one type in the modification of the external cusps into more or less distinct Vs of equal proportions, while the internal part of the crown is modified from transverse crests, such as are seen in the Toxodontia. The genera are as follows:

I. Canines one-rooted.	
? Canines; incisors small and separated by diastemata;	*Diatomicodon* Amegh.
Inferior molars with simple Vs;	*Scalabrintherium* Amegh.
Vs of inferior molars with an external transverse branch;	*Oxyodontotherium* Amegh.
II. Canines above two-rooted.	
? Canines; external nares advancing to between premaxillaries;	*Mesorhinus* Amegh.
External nares bounded by maxillaries in front;	*Macrauchenia* Ow.

But little is known of these genera, excepting Macrauchenia. In this genus there are three subequal toes, both anteriorly and posteriorly, and progression was digitigrade. The nostrils were remarkable for their posterior position, being partly above the orbits. The latter are closed behind. The last premolar teeth only in both jaws are like the molars, and there is a short diastema in front of the small canine. Incisors like those of a horse, without the cups. Dental formula: I. $\frac{3}{3}$; C. $\frac{1}{1}$; Pm. $\frac{}{4}$; M. $\frac{3}{3}$. The molars, as is often the case in the Argentine forms, soon wear so as to obscure the structure, and an internal cingulum encloses the spaces between the cross-crests as fossæ. The absence of vertebrarterial canal from the cervical vertebræ in this genus is a repetition of what occurs in the Camelidæ. Four species of Macrauchenia are described (Plate XVII.).

Macrauchenia patachonica Owen was an animal of about the proportions of a mule. The posterior position of the external nostrils has suggested that the habits were aquatic, or that it possessed a short trunk like the tapir. It is a characteristic species of the Pliocene beds of Buenos Ayres. A smaller species, *M. boliviensis* Huxley, has been found in corresponding beds in Bolivia. *Scalabrintherium paranense* Brav. and *orthii* Amegh. are from Miocene beds of the Paraña. The same formation has produced the *Mesorhinus pyramidatus* Amegh., which had the dimensions of the guanaco. No genus of the family has been yet reported from the Eocene.

The Astrapotheriidæ include the largest forms of the Litopterna, if they belong truly to this suborder. Three genera are certainly known, which differ as follows:

Dentition; I. $\frac{?}{3}$; C. $\frac{1}{1}$; Pm. $\frac{4}{4}$;
M. $\frac{3}{3}$; no diastema; *Homalodontotherium* Huxley.
Dentition; I. $\frac{3}{3}$; C. $\frac{1}{1}$; Pm. $\frac{2}{1}$;
M. $\frac{3}{3}$; a long diastema; *Astrapotherium* Burm.
Dentition; I. ?; C. ?; Pm. $\frac{1}{1}$;
M. $\frac{3}{3}$; a long diastema; *Listriotherium* Merc.

In Homalodontotherium the dental series is uninterrupted, and the canines are small and resemble simple premolars. The premolars differ somewhat from the molars, and the molar series generally has much the appearance of that of Cænopus among the rhinoceroses. In the inferior molars the resemblance is not so great, although not wanting (Fig. 4). Nothing is known of the typical and only species, *H. cunninghamii* Flower, but the dentition, and this indicates an animal of the size of an ox.

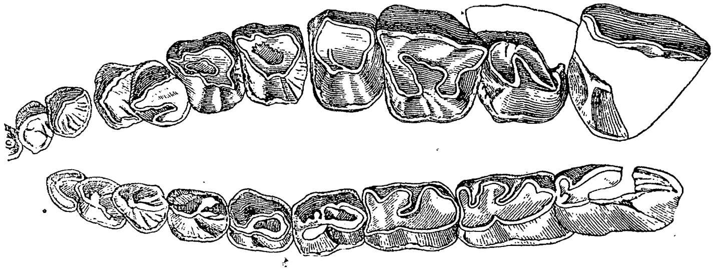
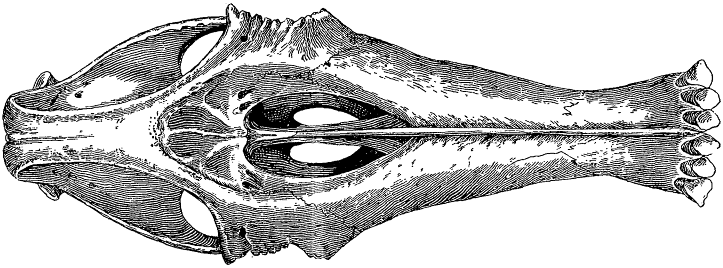


FIG. 4.—*Homaladontotherium cunninghamii* Flower; upper and lower dental series; about two-fifths natural size. From Flower.

In Astrapotherium Burm. the dentition is much more specialized. The canines are large, and they are followed by a diastema. There are only two premolars above and one below. The superior premolars differ from the true molars more than is the case with Homalodontotherium, but they have the same character, —*i. e.*, an external wall, and a curved internal crest, the convexity

PLATE XVII.



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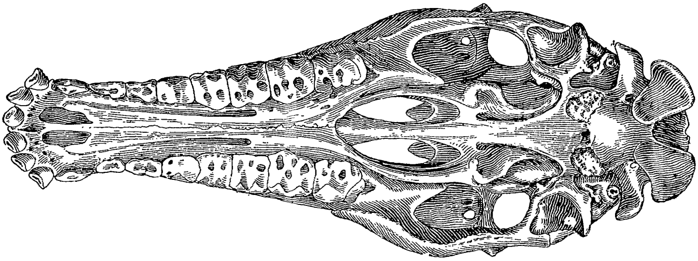

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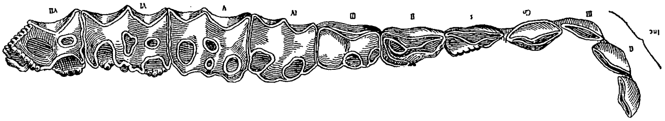

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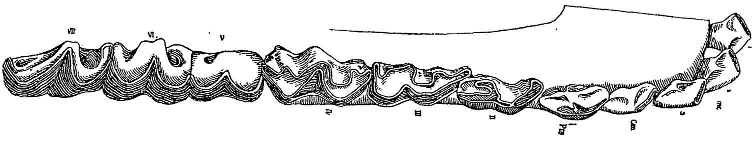

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Macrauchenia patachonica Owen.

inwards. They are much smaller than the true molars (Fig. 5). Five species are known. The *A. magnum* Owen, the largest mammal of the Eocene of South America, equals a rhinoceros in dimensions. Its canine teeth, well developed in each jaw, rendered it a formidable animal.

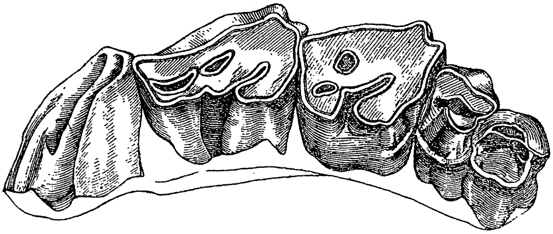

FIG. 5.—*Astrapotherium magnum* Owen; last five superior molars; about one-third natural size. From Ameghino.

All the species of the Astrapotheriidæ are from the Lower Eocene of Patagonia.

EXPLANATION OF PLATE XVII.

Macrauchenia patachonica Owen; from Burmeister; much reduced.

FIG. 1.—Skull from above.
FIG. 2.—Skull from below.
FIG. 3.—Superior dental series.
FIG. 4.—Inferior dental series.